The Osteology and Relationships of the Echelid Eel, *Kaupichthys diodontus*[1]

William A. Gosline[2]

INTRODUCTION

The main functions of the present paper are to demonstrate that two very different families of eels have hitherto been included under the "Echelidae" and to allocate these families to their proper positions in the order Anguilliformes (or Apodes). In order to establish these points, the osteology of *Kaupichthys diodontus* Schultz is dealt with in some detail.

On September 7, 1949, an unripe female of this species, 155 mm. long, was taken by Strasburg, Welsh, and the author in a poison station in shallow water off the aquarium at Waikiki, Oahu, Territory of Hawaii. The species (and genus) was originally described by Schultz (1943: 50, pl. 6 and text fig. 5*i*) from Tau and Rose Islands in the Samoan group. It is hitherto unrecorded from Hawaii. The specimen at hand differs from Schultz's description (and from a Bikini specimen dealt with below) as follows: the teeth are blunter than indicated in his diagnosis and figure (5*i*); the two rows of vomerine teeth are not so widely separated, nor do they extend farther posteriorly than the maxillary rows; and finally, the maxillary teeth are quite distinctly set apart from the premaxillary and vomerine groups. Whether the Hawaiian form merits specific or subspecific distinction, or whether the above-mentioned differences are merely individual or size variations, I do not have sufficient material to decide.

In identifying the Waikiki specimen I became doubtful as to its relationship with the other Hawaiian genus—*Muraenichthys*—which has always been placed in the same family with it (Schultz, 1943: 49; Schultz and Woods, 1949: 170). A specimen of *Kaupichthys diodontus* from Bikini, one of the duplicates very kindly sent me by Dr. Schultz, permitted an osteological investigation of that species. From this examination it is very apparent that *Kaupichthys* and *Muraenichthys* do not belong in the same family; in fact they belong on opposite sides of the major division of the eels as classified by Regan (1912) and Trewavas (1932). An account of the osteology of *Kaupichthys*, based on the 100 mm. specimen from Bikini, follows. The specimen was stained in alizarin and the head dissected; the remainder of the specimen was cleared in potassium hydroxide.

OSTEOLOGY

The lateral line canals of the body and head are enclosed in a series of small bony ossicles except where they penetrate the skull bones. That of the body gives rise to only two pores leading to the exterior; these are both forward of the pectoral (Fig. 1). In the head region the sensory canal system is of rather normal eel pattern (Trewavas, 1932, pl. 4*b* and text fig. 3A), though the number of pores leading to the surface of the head is somewhat reduced. A longitudinal canal (ll) connects the lateral line of the body with that of the head system. As is usual in eels, a transverse canal (tc) run-

[1]Contribution No. 3, Hawaii Marine Laboratory.
[2]Department of Zoology, University of Hawaii.
Manuscript received February 27, 1950.

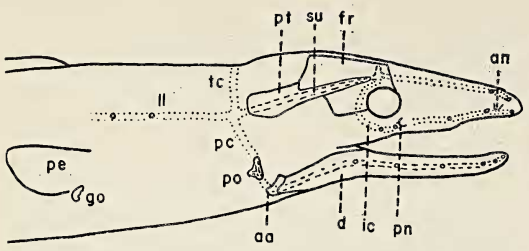

FIG. 1. Outline of head region of *Kaupichthys diodontus* indicating the course of the lateral line canals. Areas in which the canals pass through flesh are shown as dotted lines; areas in which canals pass through bone are shown in dashed lines with the outlines of the bones drawn in. Pores opening to the exterior from the canal system are shown as circles. aa, Articular-angular; an, anterior nostril; d, dentary; fr, frontal; go, gill opening; ic, infraorbital canal; ll, lateral line; pc, preopercular canal; pe, pectoral fin; pn, posterior nostril; po, preopercle; pt, pterotic; su, supraorbital canal; tc, transverse postcranial canal.

ning up and across the nape just behind the skull connects the longitudinal canals of the two sides of the body; it gives rise to a series of pit organs externally but to no pores. The preopercular canal (pc) exits ventrally from the longitudinal canal opposite the junction of the latter with the one crossing the nape and proceeds anteroventrally through the preopercle and into the articular-angular and dentary in a normal manner. The longitudinal canal itself passes forward into the head as the supraorbital canal (su), which runs the entire length of the pterotic and through a short section of the frontal; from here it passes forward in a tube—all that is left of the nasal—to the tip of the snout. In addition, a short branch runs mesially in the frontal, but does not meet its fellow from the other side, nor does it give rise to a pore to the exterior. The infraorbital canal (ic) emerges from the supraorbital system in the frontal, runs laterally and then downward behind the eye and finally forward in the upper lip to the tip of the snout; in the lip it runs mesial to the posterior nostril and below the anterior nostril. The pores opening to the exterior from the lateral line system are shown in Figure 1.

The suspensorium of *Kaupichthys* (Fig. 2) is vertically suspended, i.e., the articulation between the quadrate (q) and the articular-angular (aa) lies but slightly behind the center of the hyomandibular (h). The palatopterygoid (pp) is laminar and well developed for eels, but appears to be unattached, except by a ligament, either before or behind. The maxillary (m) articulates with the combined premaxillary, ethmoid, and vomer (ev) near the tip of the snout. The opercular apparatus is reduced. The preopercle (po), which remains chiefly as a tube for the lateral line canal, overlies the broadly wedge-shaped interopercle (io). The subopercle (sr) completely encircles the opercle (op) below. The top half of the normal fish opercle is gone, only the lower half remaining.

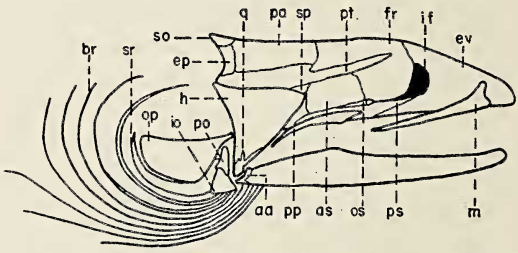

FIG. 2. Head skeleton with suspensorium, jaws, opercular bones, and branchiostegal rays. Teeth are omitted, and all the branchiostegal rays are not shown: as, Alisphenoid; br, branchiostegal ray; ep, epiotic; ev, premaxillary-ethmo-vomer; fr, frontal; h, hyomandibular; if, interorbital foramen; io, interopercle; m, maxillary; op, opercle; os, orbitosphenoid; pa, parietal; po, preopercle; pp, palatopterygoid; ps, parasphenoid; pt, pterotic; q, quadrate; so, supraoccipital; sp, sphenotic; sr, subopercle.

In the cranium (Fig. 3*a–d*) the premaxillaries are ankylosed to the ethmo-vomer. The orbitosphenoid (or) is a long, slender bone wedged between the parasphenoid (ps) below and the alisphenoid (al) and frontal above. The enlarged otic bulla (ob) is composed ventrally of the basioccipital (bo) and the prootic (pr); it contains a large sagitta

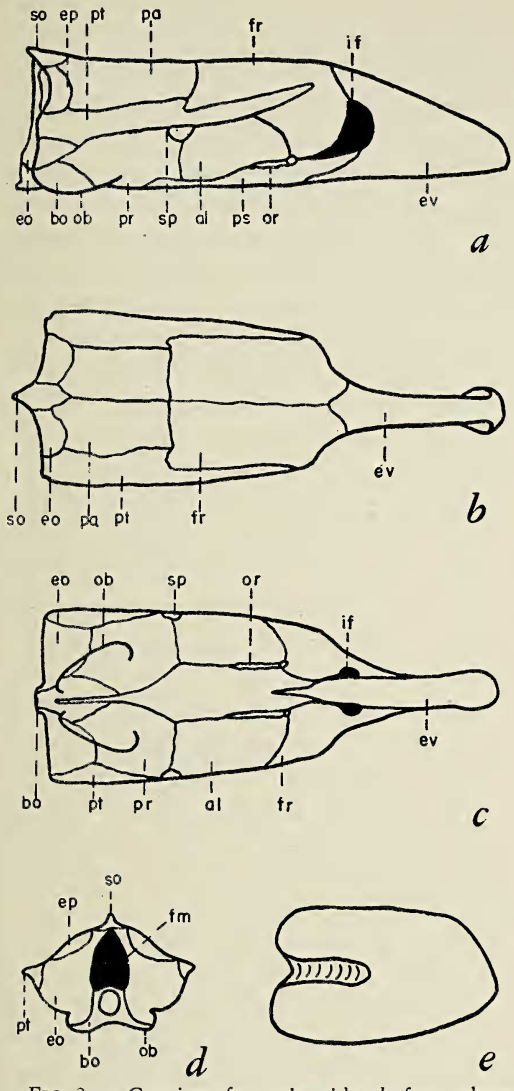

FIG. 3. *a*, Cranium from the side; *b*, from above; *c*, from below (teeth omitted); *d*, from behind; *e*, sagitta. al, Alisphenoid; bo, basioccipital; eo, exoccipital; ep, epiotic; ev, premaxillary-ethmovomer; fm, foramen magnum; fr, frontal; if, interorbital foramen; ob, otic bulla; or, orbitosphenoid; pa, parietal; pr, prootic; ps, parasphenoid; pt, pterotic; so, supraoccipital; sp, sphenotic.

(see Fig. 3*e* this paper and Frost, 1926: 99). On the dorsal surface of the skull the frontals are completely divided by suture; the parietals (pa) are rather large for eels; the pterotics are elongate. On the posterior face of the skull the foramen magnum (fm) is large and the socket for the articulation of the vertebral column relatively small for eels. The first vertebra is not fused to the skull.

The branchial apparatus (Figs. 4 and 5) is of normal eel type, without specialized features. There are 15 branchiostegal rays (br) on each side; those of the two sides of the head do not overlap on the midventral line and rather closely encircle the opercular bones behind. The upper pharyngeals (up) articulate with the upper ends of the third and fourth branchial arches. The fourth arch closely adjoins the lower pharyngeals (lp) below. Both upper and lower pharyngeals

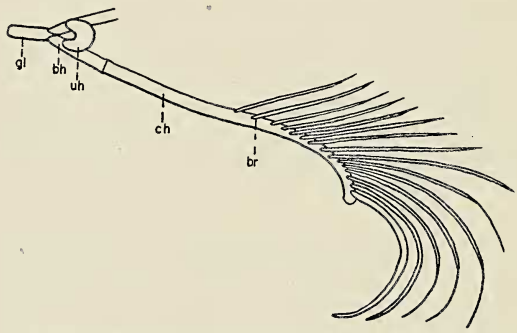

FIG. 4. Right side of hyoid arch, from below. bh, Basihyal; br, branchiostegal ray; ch, ceratohyal; gl, glossohyal; uh, urohyal.

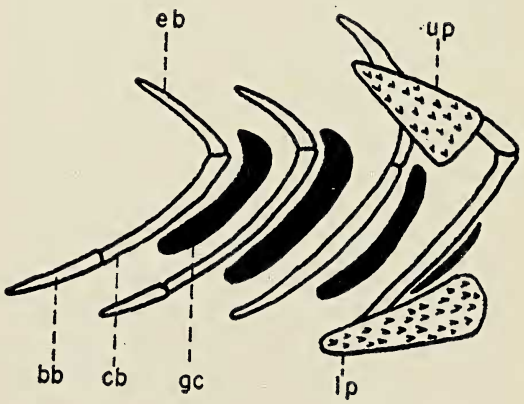

FIG. 5. Median view of right gill arches, somewhat opened out. bb, Basibranchial; cb, ceratobranchial; eb, epibranchial; gc, gill cleft; lp, lower pharyngeal; up, upper pharyngeal.

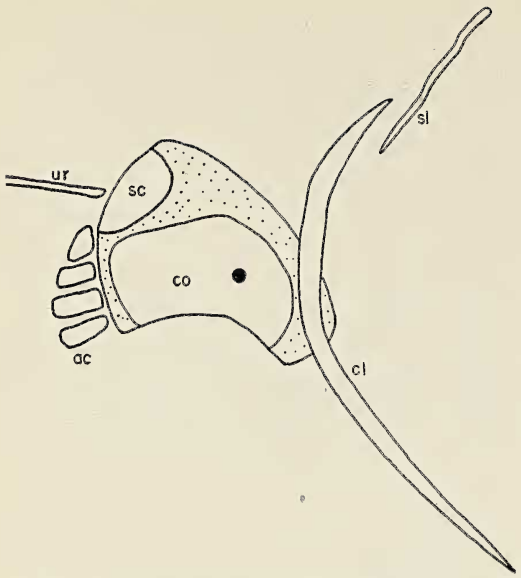

FIG. 6. Lateral view of right side of pectoral girdle. Cartilage stippled. ac, Actinost; cl, cleithrum; co, coracoid; sc, scapula; sl, supracleithrum; ur, upper pectoral ray.

bear conical teeth. The openings between the first four gill arches are wide; that between the fourth and fifth is restricted.

The pectoral girdle of *Kaupichthys* (Fig. 6) is rather well developed for eels. The supracleithrum (sl) lies free in the flesh without articulation above or below. The cleithrum (cl) is a long, curved bone overlying the forward end of the endoskeletal girdle. The coracoid (co) and scapula (sc) are embedded in a cartilaginous plate. There are four actinosts (ac), of which three and a half articulate with the coracoid area.

The vertebrae number approximately 98. Of these, about 20 lie ahead of the anus. However, the numbers of preanal and abdominal vertebrae are not the same, for the coelomic cavity of this fish extends posterior to the anus, as does the portion of the vertebral column without closed haemal arches.

The short centrum (ce) of the first vertebra (Fig. 7*a*) has a rounded head fitting the socket of the basioccipital. It bears a neural arch (na), which extends backward over the centrum of the second vertebra. The second vertebra, in addition to the neural arch, has a median ventral projection. The third is similar to the second but bears a well-developed transverse process pointing postero-laterally. The neural arches of the first few vertebrae have crests with two to several dorsal spinelets. These small spines drop out behind about the fifth vertebra. Farther back along the vertebral column each neural arch gives rise to a neural spine, these becoming well developed over the middle of the caudal portion of the vertebral column, but diminishing again posteriorly, and dropping out completely over the last nine vertebrae.

Over the whole rear part of the abdominal section of the column the vertebrae develop broad, flat, lateral flanges. These, however, fail to bear ossified ribs. In fact, there appear to be no articulated ribs anywhere in the fish. Nevertheless, there are, in the caudal section, what appear to be long, slender, unarticulated epipleurals and epineurals for each vertebra (not shown in Fig. 7*c*).

Posteriorly the haemal canal seems to stop at the seventy-eighth vertebra. The haemal spines (Fig. 7*c*, hs) continue to the ninety-third. The final vertebra (Fig. 7*b* and *d*) is extremely elongate. It appears to be made up in part of a rudimentary centrum, with neural and haemal arch, and in part of endoskeletal elements (ee) of several fin rays. These endoskeletal elements form three groups united to the rest of the vertebra by a cartilaginous plate containing a large foramen (fo).

The heart lies just behind the gill arches and immediately before the level of the pectoral girdle.

RELATIONSHIPS

The osteology of *Muraenichthys* closely resembles that of the Ophichthyidae (to be dealt with in a forthcoming paper) and differs vastly from that of *Kaupichthys* described above. The frontals of *Muraenich-*

thys are fused; the orbitosphenoid is short and rounded; the otic bulla is little developed; the parietals and pterotics are far smaller; the suspensorium is somewhat forwardly inclined; and the branchiostegal rays are long, fine, and numerous. Still other differences between the two genera are to be found in the pectoral girdle and vertebral column.

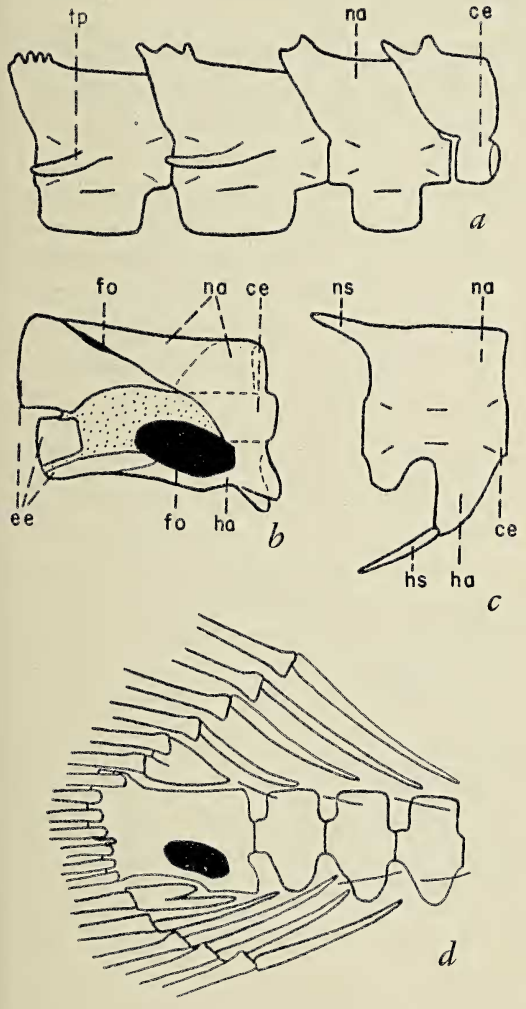

FIG. 7. *a,* First four vertebrae, lateral view of right side; *b,* terminal vertebra (cartilage stippled); *c,* seventy-ninth vertebra; *d,* last four vertebrae plus endoskeletal and bases of exoskeletal elements of fin rays. ce, Centrum; ee, endoskeletal elements of fin rays; fo, foramen; ha, haemal arch; hs, haemal spine; na, neural arch; ns, neural spine; tp, transverse process.

Since both *Muraenichthys* and *Kaupichthys* have always been included in the Echelidae, a question of the allocation of the family name arises. It is obvious from Regan's diagnosis (1912: 380 and 386) of his family Echelidae that he investigated the *Muraenichthys* type of eel. On the other hand, from the descriptions of *Echelus myrus,* the genotype of *Echelus,* given by Richardson (1844: 108), Günther (1870: 50), and Jordan and Davis (1892: 642), it appears that the family name Echelidae belongs with *Kaupichthys.* The *Muraenichthys* type can probably best be placed within the Ophichthyidae, following the suggestion of Myers and Storey (1939: 157), as a subfamily, Myrophinae. However, the final applications of the names Echelidae and Myrophinae (or Myrophidae) must await an osteological examination of *Echelus myrus,* a Mediterranean species unavailable to me.

The family Echelidae in the sense used just above, i.e., limited to the *Kaupichthys* type of eel, shows distinct relationship to the Moringuidae and Heterenchelidae in the paired frontals, and particularly in the enlarged otic bulla. It differs from either of the latter families in possessing relatively high vertical fins and labial posterior nostrils. It resembles the Heterenchelidae but not the Moringuidae in the long, narrow orbitosphenoid, in the laminar palatopterygoid, in having the trunk shorter than the tail, and, apparently, in the movable articulation between the first vertebra and the skull. It resembles the Moringuidae but not the Heterenchelidae in lacking a suture between the ethmoid and the vomer. Thus the relationships of *Kaupichthys*—and provisionally of the Echelidae—are closest with the Heterenchelidae.

The fact that *Kaupichthys* and *Muraenichthys* belong to different families also raises the problem of the family allocation of the remaining genera assigned to the Echelidae *auctorum.* Some, such as *Garmanichthys,* appear to belong with *Kaupichthys.* Others,

for example *Myrophis,* are of the *Muraenichthys* type. The superficial similarity between the two groups makes the problem of properly placing the genera particularly complex. Both have no free tongue, have the posterior nostril on the upper lip, the dorsal and anal confluent around the tip of the tail, and the gill opening consisting of a small hole. Within the Myrophinae the position of the anus and of the origin of the dorsal vary considerably, and the pectoral fin may be present (as in *Myrophis*) or absent (as in *Muraenichthys*); consequently these characters cannot be used to separate the Myrophinae from *Kaupichthys.*

The only superficial distinction that I can find between the groups is the presence in the Myrophinae of a swollen gullet supported by a basket-like arrangement of the numerous, long branchiostegal rays (Parr, 1930: 71), and the absence of these characters in the *Kaupichthys* type of eel. Other distinguishing external characters could probably be found if adequate comparative material were available.

REFERENCES

Frost, G. A. 1926. A comparative study of the otoliths of the neopterygian fishes. III. Apodes. *Ann. and Mag. Nat. Hist.* IX, 17: 99–104.

Günther, A. 1870. *Catalogue of the fishes of the British Museum.* Vol. 8, xxv + 549 pp. Taylor and Francis, London.

Jordan, D. S., and B. M. Davis. 1892. A preliminary review of the apodal fishes or eels inhabiting the waters of America and Europe. *Rept. U. S. Fish Comm. 1888,* 16: 581–677, pls. 73–79.

Myers, G. S., and M. H. Storey. 1939. *Hesperomyrus fryi,* a new genus and species of echelid eels from California. *Stanford Ichthyological Bul.* 1 (4): 156–159, fig. 1.

Parr, A. E. 1930. Jugostegalia, an accessory skeleton in the gill cover of the eels of the genus *Myrophis. Copeia 1930:* 71–73, fig. 2.

Regan, C. T. 1912. The osteology and classification of the teleostean fishes of the order Apodes. *Ann. and Mag. Nat. Hist.* VIII, 10: 377–387, figs. 1 and 2.

Richardson, J. 1844. *The zoology of H. M. S. "Erebus" and "Terror." Fishes.* 139 pp., 38 pls. London.

Schultz, L. P. 1943. *Fishes of the Phoenix and Samoan Islands.* U. S. Natl. Mus. Bul. 180. x + 316 pp., 9 pls., 27 figs., 32 tabs.

——— and L. P. Woods. 1949. Keys to the genera of echelid eels and the species of *Muraenichthys* of the Pacific, with two new species. *Wash. Acad. Sci., Jour.* 39 (5): 169–174, 2 figs., 1 tab.

Trewavas, E. 1932. A contribution to the classification of the fishes of the order Apodes, based on the osteology of some rare eels. *Zool. Soc. London, Proc. 1932:* 639–659, pls. 1–4, 9 figs., 1 tab.